Gas exchange responses to CO_2 concentration instantaneously elevated in flag leaves of winter wheat cultivars released in different years

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Abstract

Three winter wheat (*Triticum aestivum* L.) cultivars, representatives of those widely cultivated in Beijing over the past six decades, were grown in the same environmental conditions. Net photosynthetic rate (P_N) per unit leaf area and instantaneous water use efficiency (WUE) of flag leaves increased with elevated CO_2 concentration. With an increase in CO_2 concentration from 360 to 720 μmol mol^{-1}, P_N and WUE of Jingdong 8 (released in 1990s and having the highest yield) increased by 173 and 81 %, while those of Nongda 139 (released in 1970s) increased by 88 and 66 %, and Yanda 1817 (released in 1945, with lowest yield) by 76 and 65 %. Jingdong 8 had the highest P_N and WUE values under high CO_2 concentration, but Yanda 1817 showed the lowest P_N. Stomatal conductance (g_s) of Nongda 139 and Yanda 1817 declined with increasing CO_2 concentration, but g_s of Jingdong 8 firstly went down and then up as the CO_2 concentration further increased. Intercellular CO_2 concentration (C_i) of Jingdong 8 and Nongda 139 increased when CO_2 concentration elevated, while that of Yanda 139 increased at the first stage and then declined. Jingdong 8 had the lowest C_i of the three wheat cultivars, and Yanda 1817 had the highest C_i value under lower CO_2 concentrations. However, Jingdong 8 had the highest P_N and lowest C_i at the highest CO_2 concentration which indicates that its photosynthetic potential may be high.

Additional key words: C_i; C_i/C_a; net photosynthetic rate; stomatal conductance; water use efficiency; transpiration rate.

Introduction

Photosynthetic rate of most of C_3 plants increases with the increase in CO_2 concentration, while that of C_4 plants levels off (Akita and Moss 1973, Kimball 1983, Cure and Acock 1986, Ehleringer *et al.* 1991, Nie *et al.* 1992, Alberto *et al.* 1996, Chen *et al.* 1996, Poorter *et al.* 1996). The increased CO_2 uptake in C_3 plants is primarily due to the fact that the increased substrate concentration at the active site of the primary carboxylase, ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBPCO), suppresses photorespiration (Bowes 1996, Drake *et al.* 1997). However, the effect of CO_2 concentration enrichment varies highly among C_3 species (Jones *et al.* 1984, Rowland-Bamford *et al.* 1991) and even among different cultivars of the same crop (Ramachandra Reddy *et al.* 1993, Reddy *et al.* 1997). Several studies with wheat showed an increment in biomass and yield of about 10–20 % under CO_2 enrichment (Havelka *et al.* 1984, Mitchell *et al.* 1993, McKee and Wooodward 1994, Tuba *et al.* 1994, Weigel *et al.* 1994). This is much less than in many other crop species (30~40 %: Kimball 1983, Poorter 1993). The average CO_2-related increments in biomass and grain yield differ much between old and modern spring wheat (*Triticum aestivum* L.) cultivars (Manderscheid and Weigel 1997, Jiang *et al.* 2000).

Although there have been many investigations on the response of photosynthesis to the elevated CO_2 in high plants, the response of different winter wheat cultivars that were released in different years was seldom reported. Therefore we selected three winter wheat cultivars with different photosynthetic characteristics and yield, repre-

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Abbreviations: C_a – ambient CO_2 concentration; C_i – intercellular CO_2 concentration; E – transpiration rate; g_s – stomatal conductance; P_i – phosphoric acid; P_N – net photosynthetic rate; PPDF – photosynthetic photon flux density; RuBP – ribulose-1,5-bisphosphate; RuBPCO – ribulose-1,5-bisphosphate carboxylase; WUE – instantaneous water use efficiency.
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sentatives of those widely cultivated in Beijing over the passed six decades, and investigated their gas exchange response to CO_2 concentration increase in the field. The question was how photosynthesis acclimates to elevated CO_2 concentration and how it varies in hereditarily improved wheat cultivars.

Materials and methods

Plants: Three winter cultivars of *T. aestivum*, representatives of those widely cultivated in Beijing over the passed six decades (Table 1), were Yanda 1817 (released in 1940's), Nongda 139 (released in 1970's), and Jingdong 8 (released in 1990's). The experiment was done in the Experiment Farmland of Beijing Academy of Agroforestry (39°09'N, 116°04'E) in 2000-2001. The major elements of soil were: total nitrogen (N) 0.171 %, available N 57.6 mg kg^{-1}, available P 85.1 mg kg^{-1}, and K 110.0 mg kg^{-1}. All the cultivars received the same agricultural management, such as watering, fertilising, and pesticides. All growing environments were similar to those in the agriculture fields of Beijing area, North China. The low yield cultivars are always taller, which makes them easy to fall down. Wood stick supports (100×250×40 cm, height×length×depth) were used to prevent lodging, in order that the ultimate yield potential could be reached. With the help of such simple constructions, the low yield cultivars had successfully finished their development stages without lodging.

Table 1. List of representative cultivars of winter wheat released in different eras of the last century, with grain yield records, increase rates, grain yield, biomass, and harvest index.

Cultivar	Yanda 1817	Nongda 139	Jingdong 8
Released in the year	1945	1983	1995
Yield [g m^{-2}]	65	275	583
Increase in yield [%]	-	323	797
Grain yield [g m^{-2}]	420	448	546
Biomass [g m^{-2}]	1233	1111	1192
Harvest index	0.34	0.40	0.45

Gas exchange: Two separate 4 000 cm^3 steel bottles (9.5 MPa) containing 0 or 1 000 μmol(CO_2) mol^{-1} were ordered from *Beijing AP Beifen Gas Industry Co.* The oxygen concentration of both bottles was 21 %, using N_2 as buffer gas. Mixing the two kinds of gases in different proportions produced five CO_2 concentrations, which were put into five plastic bags (10 000 cm^3). The CO_2 concentration in each bag was measured by an *LCA-4* portable photosynthesis system (*ADC*, Hoddesdon, UK). CO_2 concentrations of 360, 500, 570, 650, and 720 μmol mol^{-1} (mentioned here as C_{360}, C_{500}, C_{570}, C_{650}, and C_{720}) were produced and applied to the selected cultivars.

For measurements at the beginning of May, fully developed flag leaves in middle to upper crown were used. We chose as clear and windless days as possible. P_N, transpiration rate (E), C_i, and g_s were measured under different CO_2 concentrations using the *LCA-4* system. WUE was calculated as P_N/E. We firstly linked the bag full of gas of needed CO_2 concentration with the gas input aperture of the *LCA-4*. When the CO_2 concentration was stable, we started to measure gas exchange. Three replications were made on each cultivar in different location of the field, and five data sets of each measurement were recorded. All plants were harvested at the maturity and the grain yield was determined.

Data analysis: The large data set was entered into an *Excell* spread sheet, which included cultivars, time, physiological measurements, leaf areas, and sites. Analysis of variance of leaf traits was carried out on each measurement and the significance of cultivars mean square determined by testing against the error (cultivars×replicate) mean square. Then all results of analysis were entered into *Sigmaplot* to create the graph. The primary data set was copied into a *SPSS* sheet to make correlation analysis.

Results

Response of P_N to CO_2 concentration: P_N in flag leaves of all three wheat cultivars increased with CO_2 concentration (Fig. 1*A*). The promotion of P_N of Jingdong 8 was larger (by 173 %) than that of the other two cultivars, Nongda 139 and Yanda 1817 (88 and 76 % increment, respectively, at C_{720}). For Jingdong 8 the P_N *vs.* CO_2 concentration dependence was exponential, indicating that CO_2 saturation of P_N lied much higher than 720 μmol mol^{-1}. However, P_N of the other wheat cultivars increased more slowly as the CO_2 concentration increased. Thus P_N of Yanda 1817 was maximal at C_{720}. At C_{360}, P_N of Jingdong 8 was slightly lower but at higher CO_2 concentrations much higher than that of the other two cultivars. P_N of Yanda 1817 was the lowest under all the CO_2 concentrations.

Response of E to CO_2 concentration: E in flag leaves slightly increased with increase in CO_2 concentration (Fig. 1*B*). Nongda 139 had the highest E of all three cultivars, while Jingdong 8 maintained the lowest E under C_{360} to C_{500}. In Jingdong 8, E went up quickly and became the highest at C_{720} (a 50 % increase between C_{500} and C_{720}). This was consistent with the response of g_s to CO_2 concentration (Fig. 1*C*). E of Yanda 1817 increased slightly with the increase in CO_2 concentration, but E of Nongda 139 fluctuated at increased CO_2 concentrations.

Response of g_s to CO_2 concentration: g_s in flag leaves of wheat tended to decline with increase in CO_2 concentration, especially in Yanda 1817 at C_{720} (Fig. 1*C*). Nongda 139 had the highest g_s values of the three cultivars within the range C_{360} to C_{570}. However, Jingdong 8 had the highest g_s value at C_{720} because it went up starting with C_{500}, while g_s of the other two cultivars went down. Under higher CO_2 concentrations, a sharp increase in P_N in leaf of Jingdong 8 was related to increase in g_s (p<0.01, Table 2).

Table 2. Pearson correlation analysis of physiological variables and CO_2 concentration. ***Correlation is significant at the 0.001 level (2-tailed) (n = 149). **Correlation is significant at the 0.01 level (2-tailed).

	Ca	E	g_s	P_N	Ci	WUE	Ci/Ca
C_a	1.000	0.493***	-0.488***	0.878***	0.508***	0.864***	-0.575***
E		1.000	0.268***	0.666***	0.414***	0.263***	-0.102
g_s			1.000	-0.214**	0.100	-0.465***	0.650***
P_N				01.000	0.289***	0.889***	-0.649***
C_i					1.000	0.151	0.395***
WUE						1.000	-0.780***
C_i/C_a							1.000

Response of WUE to CO_2 concentration: WUE of all the three wheat cultivars went up as the CO_2 concentration increased (Fig. 1*D*). WUE of Jingdong 8 was the highest, and the difference in WUE between Yanda 1817 and Nongda 139 was small and inconsistent. WUE of Yanda 1817 was mostly higher than that of Nongda 139.

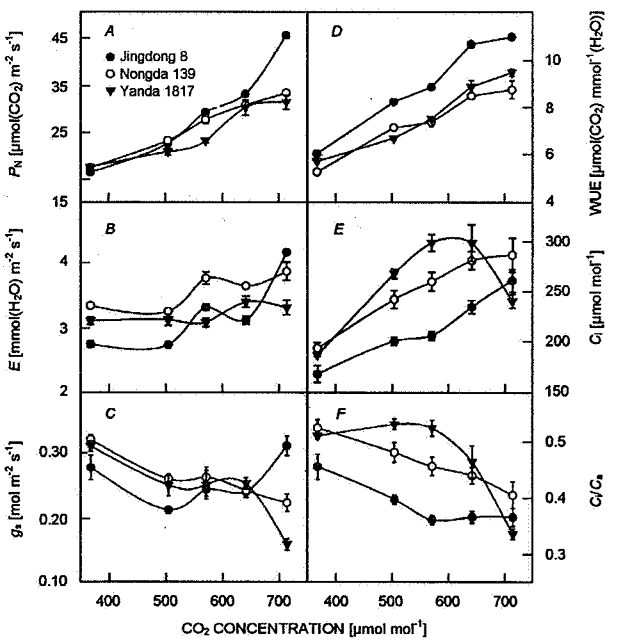

Fig. 1. Responses of gas exchange parameters [A – net photosynthetic rate (P_N), B – transpiration rate (E), C – stomatal conductance (g_s), D – instantaneous water use efficiency (WUE), E – intercellular CO_2 concentration (C_i), F – ratio of C_i to ambient CO_2 concentration (C_i/C_a)] in flag leaves of three wheat cultivars to elevated CO_2 concentration. Means ± SE, n = 15.

Jingdong 8 had a higher WUE due to high P_N and low E, it improved its WUE by 81 % in the range C_{360} to C_{720}, while Nongda 139 and Yanda 1817 increased theirs by 66 and 65 %, respectively. Thus Jingdong 8 can use water very economically under high CO_2 concentrations.

Response of C_i to CO_2 concentration changes: C_i also increased with increase in CO_2 concentration (Fig. 1*E*). Among the three cultivars, Jingdong 8 had the lowest C_i, while Yanda 1817 had the highest one. C_i of Jingdong 8 increased by 55.0 % when CO_2 concentration changed from C_{360} to C_{720}, but that of Nongda 139 increased by 47.7 %. In Yanda 1817 the increase was by 59.8 % in the range C_{360} to C_{570}, followed by a rapid decline in the range C_{650} to C_{720}. However, the former two cultivars increased their C_i values linearly with the increase in CO_2 concentration. Thus, the lower P_N in flag leaves of Yanda 1817 might be caused by the lower ability of RuBPCO for assimilation instead of the lower g_s. On the contrary, because of the lower ability of RuBPCO, Yanda 1817 could consume less CO_2 under high CO_2 concentration, thereby C_i of Yanda 1817 was increased quickly which led to a sharp decrease in g_s. P_N in leaves of Jingdong 8 increased rapidly as the CO_2 concentration was elevated and low C_i was kept. Therefore, g_s in leaves of Jingdong 8 increased with the increase in CO_2 concentration.

Response of C_i/C_a to CO_2 concentration: This ratio declined in the three wheat cultivars with increase in CO_2 concentration (Fig. 1*F*). However, there were big differences in the shape of curves of CO_2 concentration *vs.* C_i/C_a of the three wheat cultivars: C_i/C_a of Yanda 1817 increased slightly within C_{360} to C_{570}, then decreased much when CO_2 concentration further increased. C_i/C_a of Nongda 139 went down linearly with CO_2 concentration, while that of Jingdong 8 declined rapidly in the range C_{360} to C_{570}, then it increased slightly when the CO_2 concentration further increased. Jingdong 8 had the lowest C_i/C_a values of the three cultivars, and Nongda 139 had the highest ones. However, the decline in C_i/C_a of Nongda 139 was caused by low g_s (Table 2, Fig. 1*C*), while that of Jingdong 8 by sharp increase in P_N.

Correlations of physiological variables and CO_2 concentrations: Almost all of the Pearson corrections among C_a, P_N, E, g_s, C_i, WUE, and C_i/C_a (Table 2) were significant. Thus E, P_N, C_i, and WUE were positively correlated with C_a ($p<0.001$), g_s and C_i/C_a were negatively correlated with C_a ($p<0.001$). g_s, P_N, C_i, and WUE were negatively correlated with P_N and WUE ($p<0.001$), and positively correlated with C_i/C_a ($p<0.001$). P_N was significantly positively correlated with C_i and WUE, and negatively correlated with C_i/C_a ($p<0.001$). C_i/C_a was negatively correlated with WUE, and positively correlated with C_i ($p<0.001$).

Discussion

Different cultivars of the same crop respond often differently (Ramachandra Reddy *et al.* 1993, Mandersheid and Weigel 1997, Reddy *et al.* 1997) to CO_2 concentration. We found that P_N of the three wheat cultivars increased as the CO_2 concentration was elevated. P_N of Jingdong 8 increased much more than that of the other two cultivars, which suggested that photosynthesis in leaves of modern winter wheat cultivars adapts better to CO_2 concentration than the older ones. This is inconsistent with the result of Mandersheid and Weigel (1997) who believe that the result of CO_2 enrichment is larger growth stimulation in the old spring wheat cultivars than in the modern ones. Different environment may cause this difference. Our experiments were carried out in fertile soil in an open field, but in their study wheat was planted in small pots which may restrict P_N under high CO_2 concentration. Wall *et al.* (2000) suggest that CO_2 enrichment increases the daily integral of net leaf carbon accumulation by 30 % at high N, but only by 23 % at low N. Modern wheat cultivars acclimate to well fertilised soil, while the old ones need only much less fertiliser. For example, in our experiment the old wheat cultivars would lodge under well-irrigated and fertilised conditions if we would not protect them. Short-term elevation of atmospheric CO_2 concentration can stimulate carbon gain in C_3 plants because of increased substrate availability for the primary carboxylase, RuBPCO (Long and Drake 1991, 1992, Sage 1994, Van Oosten and Besford 1994, Woodrow 1994, Webber *et al.* 1995) and suppressed photorespiration (Sharkey 1988). Ramachandra Reddy and Gnanam (2000) considered that the observed increase in P_N was a result of elevated CO_2 concentration, attributed to reduction in photorespiration, which represents a significant loss (25 %) of previously fixed carbon in all C_3 plant. However, in our experiments P_N increased between C_{360} and C_{720} by as much as 76 % in Yanda 1817 and by 173 % in Jingdong 8. Therefore we suggest some other mechanism of photosynthetic response to elevated CO_2, especially to instantaneous CO_2 enrichment, because reduction in photorespiration alone may not lead to such great increment of P_N. The mechanism has to be further investigated.

Stomata partly close in response to elevated CO_2 (Mott 1990) which lowers g_s (Jones and Mansfield 1970, Farquhar *et al.* 1978, Morison and Gifford 1984, Morison 1985, Knapp *et al.* 1994, Adam *et al.* 2000) and leads to reduced E (Pallas 1965, Kimball and Idso 1983, Cure and Acock 1986, Tuba *et al.* 1994). However, in our study g_s of Yanda 1817 and Nongda 139 went down, but that of Jingdong 8 firstly went down and then went up again when CO_2 concentration was raised. E also increased as CO_2 concentration was elevated. This phenomenon might be related to irradiance increase at the latter measured time. In this experiment, we measured gas exchange under natural irradiation in the field, with the low CO_2 being applied earlier than the higher ones. Both the irradiance and temperature were increased while we measured gas exchange under high CO_2, which might affect g_s and E, and saturating PPDF might be increased too. Moreover, high CO_2 might not decrease g_s (Field *et al.* 1995). Anyway, stomata acclimation to high CO_2 concentration may be found in Jingdong 8 under some environmental conditions. Because we measured always under saturating PPDF, P_N might be changed only little by irradiance. The curve of P_N changes in leaves of Jingdong 8 was different from that for other cultivars, which was similar to an exponential curve instead of a logarithmic one. It indicated that the saturating CO_2 concentration was far beyond the concentrations that we used, or the saturating irradiance became higher under high CO_2 concentrations. Sionit *et al.* (1982) suggest that plants grow more quickly under high CO_2 and high irradiance than under only one of them. Photosynthesis is usually limited by one of the three general processes: (*1*) The capacity of RuBPCO to consume RuBP in CO_2 fixation. (*2*) The capacity of thylakoid reactions to supply ATP and NADPH for RuBP regeneration. (*3*) The capacity of starch and sucrose synthesis to utilise triose photophosphorylation (Farquhar *et al.* 1980, Shakey 1985, Harley and Shakey 1991). Under saturating irradiance, RuBPCO capacity limits P_N at low C_i, RuBP regeneration is the limiting factor at intermediate C_i, but P_i regeneration becomes a limiting one at high C_i. P_N of Jingdong 8 increased sharply with CO_2 concentration, which indicated that potential of photosynthesis was high. Thereby, it could consume more CO_2 under high CO_2 concentration than the other two cultivars, and slowed down the speed of C_i increase as C_a was elevated. So it could maintain lower C_i but higher g_s, because stomata were sensitive to C_i and not sensitive to C_a if C_i exerted little change (Mott 1988).

In conclusion, P_N and WUE in flag leaves of Jingdong 8 increased more quickly than those in the other two wheat cultivars, and Jingdong 8 maintained a higher g_s and lower C_i as C_a increased. We consider that the photosynthetic potential ability of Jingdong 8 is much higher than that of the other two cultivars. In other words, some photosynthetic characteristics were improved during the improvement process of wheat cultivars over the past six decades. Jingdong 8 might act much better than Nongda 139 and Yanda 1817 under higher CO_2 concentration when global change occurs.

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